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THE SEEDLING OF HAMAMELIS VIRGINIANA L.

THEO. HOLM

(Plates 206 and 207)

SEEDLINGS of trees and shrubs generally show a very uniform development, and the deviations depend mainly on the cotyledons being epigeic or hypogeic, and on the shape of the primary leaves, which sometimes differ from that of the mature tree or shrub. The internal structure, on the other hand, exhibits frequently several points of interest, and especially with regard to the early appearance of certain structural characters, which become more or less modified in the mature plant. The secondary increase in thickness of the primary root and the stem, including the hypocotyl, naturally involves several changes in the structure, beside that the tissues of the leaf are frequently subject to modification, when being exposed to change of environment, shade and light especially.

Seedlings of *Hamamelideae* are not mentioned by Lubbock;¹ he figures and describes *Bucklandia propulnea* R. Br., but this genus is a member of *Liquidambareae* according to Baillon. In *Hamamelis Virginiana* the first leaf of the seedling (FIG. 2) is large for the size of the plant, subcordate, acuminate, and distinctly crenate; the second leaf (FIG. 3) is much smaller, ovate and short-pointed; in the ultimate leaves (FIG. 1) the crenation is less pronounced, the base is oblique, and the apex varies from short-pointed to almost obtuse. The average size of the ultimate leaves aggregates about 9 cm. in length, and 6 cm. in width, but occasionally the inflorescences may be subtended by leaves measuring up to 13½ cm. in length, and 10 cm. in width. The

¹ Lubbock, John. A Contribution to our Knowledge of Seedlings. Vol. 1, London, 1892, p. 521.

vernation is not "involute" as stated by Sargent (Silva, V: 1893), but "plicate." When comparing the internal structure of the seedling, during the first season, with that of the mature tree (or tall shrub), the development of the various tissues may be described as follows.

THE ROOT-SYSTEM

In the primary root of the young seedling at the stage figured (FIG. 2), collected early in May, increase in thickness has already taken place, but only within the stele; the peripheral tissues from the epidermis to endodermis incl. are still intact. The epidermis is very small-celled, destitute of hairs, and the cell-walls are of a deep brown color; there is a thin-walled exodermis, well marked by the lumen being somewhat wider than that of the adjoining cortex. The cortical parenchyma consists of eight compact strata of roundish cells with no contents of starch or crystals; the endodermis is well preserved, thin-walled and relatively large-celled, but contains no starch. At the expense of most of the pericambium the stele presents a dense mass of leptome and hadrome in deep rays with several strata of typical libriform, enclosing a narrow, slightly thick-walled pith. In the capillary, lateral roots of the same specimen the stele shows the original structure, which is diarch; the cortex presents a narrower zone, but otherwise the structure is as described above.

At the close of the first season the primary root has grown to a considerable length, and increased in thickness. The peripheral tissues from epidermis to endodermis, inclusive, have been replaced by many strata of homogeneous, thin-walled cork of the usual structure, and by a secondary thick-walled cortical parenchyma of only two layers, containing large deposits of starch, both tissues having originated from the pericambial meristem. The stele shows the same structure as described above, but the libriform is more thick-walled.

If we compare now the older roots of mature specimens, of the flowering shrub, for instance, we notice a somewhat modified structure. The cork and the secondary cortex represent broader zones, the latter containing starch in abundance, beside large, single rhombic crystals of calcium-oxalate. Moreover, we notice a number of isolated stereids and sclereids scattered throughout this parenchyma, beside some more definite strands of stereome outside the leptome. With regard to the medullary rays these contain large, single crystals and starch. The libriform shows a somewhat peculiar structure, the cells having

an inner, quite thick, gelatinous layer, more or less separated from the lignified part of the cell-wall, thus representing the so-called "Gallert-schicht," described by De Bary;¹ it is a structure of somewhat irregular occurrence, being not exhibited by all the libriform-cells in many plants. As a matter of fact, De Bary calls attention to the occurrence of such cells together with normal libriform in the same annual ring of the trunk of certain trees, and a like variation exists also in roots. For in our *Hamamelis* we found such cells quite frequent in the innermost strata of the hadrome in the root, intermixed with normal libriform. Characteristic of the root structure is thus the early increase within the stele of the primary root of the seedling, while the peripheral tissues are still intact, succeeded during the first autumn by the replacement of these tissues by cork and a secondary cortical parenchyma. In roots of the mature tree stereids and sclereids appear in the secondary cortex, and part of the libriform shows the peculiar, gelatinous, inner layer, recorded by De Bary from the trunks of certain trees.

THE STEM

The hypocotyl of the young seedling is tall, cylindric, perfectly glabrous, but not smooth, the cuticle forming numerous, longitudinal ridges from base to apex. The epidermis is thick-walled (the outer wall), and a thin-walled cork of three strata has developed from hypodermal callenchyma (FIG. 4); the cork-cells show the general form, being stretched tangentially. The cortex is heterogeneous, consisting of two to three strata of collenchyma and of about six compact layers of thin-walled parenchyma, of which the three peripheral strata are rich in chlorophyll. There is a distinct, thin-walled endodermis, containing starch; the pericycle is composed of isolated strands of stereome in two to three layers interspersed with thin-walled parenchyma. The stele represents a compact cylinder of leptome, cambium and deep rays of hadrome with narrow, medullary rays (1-2 rows), and some libriform, slightly thick-walled. The pith is thin-walled, solid, rich in starch.

The epicotyl, the only internode of the young seedling, is obtusely triangular, and hairy with stellate hairs; the cuticle and the epidermis show the same structure as in the hypocotyl, but no cork is developed; the cortex is heterogeneous as described above, but several of the cells

¹ De Bary, A. Vergleichende Anatomie der Vegetations-organe der Phanerogamen und Farne. Leipzig, 1877, p. 497.

contain a brown substance, and large aggregated crystals of calcium-oxalate. The endodermis, pericycle and stele show the same structure as described above, but the outline of the stele is triangular, the three primordial mestome-strands being much thicker than the interfascicular.

At the close of the first season several (4-5) internodes have been developed, and in these the epidermis has become somewhat compressed, covering a broad zone of thin-walled cork, the cells of which are stretched radially as shown in FIGURE 6. The cortex consists of collenchyma and thick-walled parenchyma, both containing crystals, single in the former, but single and aggregated in the latter, besides deposits of starch. No endodermis could be distinguished, but a closed pericycle of stereome in about three layers. The stele shows the same structure as in the young seedling, but the libriform and the pith are thick-walled; the latter contains starch.

In passing to describe the structure of the branches of the mature shrub or tree, the long, slender internodes of a branch, about nine months old, show the epidermis still preserved, thick-walled and small-celled, covering four thin-walled layers of cork with the cells radially stretched (FIG. 6). The cortex is of five hypodermal strata of collenchyma surrounding three strata of moderately thickened parenchyma, of which several cells contain a brown, amorphous substance; while only single crystals were observed in the collenchyma, both single and aggregated were found in the parenchyma. No endodermis could be distinguished, but an almost continuous pericycle of three to four strata of stereome intermixed with sclereids; the sclereids showed the inner cell-wall beginning to become gelatinous. Corresponding with the circular outline of the branch (in cross-section) the stele is almost round, but shows the three primary mestome-strands very plainly. The mestome is very compact, and libriform is especially well represented in the interfascicular tissue. A large, small-celled and thick-walled endoxyle covers the inner face of the three primary mestome-strands. With regard to the leptome this contains much thin-walled parenchyma forming rays between the strands of sieve-tubes, frequently containing a brown substance, but neither starch nor crystals; the hadrome contains much libriform, beginning to show the gelatinous structure of the inner cell-wall; the vessels are relatively narrow, polyedric rather than circular in cross-sections, and the medullary rays are of only one to two rows. The pith is thick-walled, and con-

tains starch besides a brown substance, but no crystals. Viewed in longitudinal sections the cork-cells are high, but very narrow; the sclereids form long rows between the stereids, and the crystals are contained in cells, forming continuous rows, generally close to the stereome; the libriform shows bordered pits very distinctly.

This structure recurs in the older branches with the exception, that a secondary cortical parenchyma has developed on the inner face of the pericycle, and contains single crystals of calcium-oxalate. Moreover the pith shows the cells very thick-walled, porous, and stretched radially, containing several aggregated crystals, but no starch.

The three-flowered peduncle is at the time of the flowering densely hairy with numerous stellate hairs, and the cross-section is circular with a circular stele. The cortical parenchyma is homogeneous, collenchymatic, and of 12–14 layers, containing both types of crystals. The endodermis is fairly distinct, but destitute of starch, and no pericycle is developed.

Among the structures characteristic of the stem, when examined from the seedling stage to the mature tree, the following may be mentioned. The cuticle forming longitudinal ridges on the hypocotyl and the epicotyl; the absence of hairs from the hypocotyl; the development of stellate hairs on the epicotyl and subsequent internodes; the development of cork beginning in the young hypocotyl; the cortex being heterogeneous, *i. e.* collenchymatic and parenchymatic in the hypocotyl and in all the succeeding internodes, except in the floral peduncle, where the cortex is collenchymatic all through; endodermis being distinct in the hypocotyl, epicotyl and in the floral peduncle, but absent from the other internodes; the pericycle being purely stereomatic in the seedling, but interspersed with sclereids in the young branches of the tree, and absent from the floral peduncle; the stereids and the libriform showing a gelatinous, inner wall in the branches of the tree; a well-developed endoxyle in the young branches of the tree; the cells of the pith being very thick-walled and stretched radially (in cross-sections) in old branches. The distribution of crystals of calcium-oxalate is very unequal: *viz.*, none in the hypocotyl; aggregated in the cortex and pith of the epicotyl; single crystals in the cortex of the apical internodes of the seedling during the autumn; single and aggregated in the lower internodes during autumn; aggregated and single in the primary parenchymatic cortex of young

branches of the tree; single in the collenchymatic; aggregated in the pith and primary cortex of old branches of the tree; single in the secondary cortex of all branches; single and aggregated in the collenchymatic cortex of the floral peduncle.

THE LEAVES

The relatively large, epigeric cotyledons (FIG. 2) have short petioles, which, at the characteristic point, *i. e.* just beneath the leaf-blade, are triangular in cross-section, and destitute of hairs. The cuticle is wrinkled on both faces, and the outer wall of epidermis is slightly thickened. The cortex consists of 15–20 strata of roundish cells rich in chlorophyll, and several cells contain a brown substance, but no crystals were observed; the hypodermal stratum of cortex is slightly collenchymatic on the dorsal face. The three mestome-strands are collateral and situated in a single band close to each other; a starch-bearing endodermis covers the leptome-side, and inside the endodermis are three arches of thin-walled stereome corresponding with the leptome. The blade of the cotyledon is also glabrous, and covered by a thin, smooth cuticle; the epidermis is thin-walled in the lateral parts of the blade, but slightly thick-walled (the outer cell-wall) above and beneath the midrib. Viewed in superficial sections the lateral cell-walls of epidermis are undulate on both faces of the blade, especially on the dorsal face; the stomata are confined to the dorsal face, with generally one rectangular subsidiary cell and four ordinary epidermis-cells. A few strata of collenchyma, hypodermal, are located beneath the midrib, passing into a small water-storage tissue of two to three strata. The chlorenchyma consists of one ventral stratum of very short and plump palisade-cells, some of which show the peculiar funnel-like shape, which recurs, but much more frequently, in the first green leaf succeeding the cotyledons; this stratum contains much more chlorophyll than the adjoining pneumatic tissue, which consists of about eight layers of oblong to roundish cells with wide intercellular spaces; the palisade-tissue passes uninterruptedly across the midrib. The midrib contains a single, arch-shaped, collateral mestome-strand, of which the leptome is supported by an arch of thin-walled stereome; no crystals of calcium-oxalate were observed in the cotyledon.

The primary leaf of the young seedling (FIG. 2) has a short petiole, which is hemicylindric in cross-sections, the ventral face flat; it is hairy on both faces with stellate hairs. The cuticle is thin, nearly

smooth, and the epidermis is slightly thick-walled. The cortex consists of five to six strata of thin-walled, roundish cells with chlorophyll, but no collenchyma was observed. The mestome-strands form a stele, almost circular in cross-section, and surrounded by a continuous sheath of stereome in three to four layers; a relatively broad, thin-walled pith occupies the center of the stele, containing a little starch, but no crystals. The leaf-blade of the primary leaf of same seedling shows a typical dorsiventral structure as to stomata and chlorenchyma. The cuticle is thin, smooth; the stomata are confined to the dorsal face; they are slightly raised, and have a wide air-chamber; they show three distinct structures: they are surrounded by five cells of which two are rectangular and parallel with the stoma, the others being ordinary epidermal cells with undulate lateral walls; or only one cell is rectangular, the other four being larger and with the lateral walls undulate; or there are only four cells, of which the two are much smaller than the others, but of irregular shape, and with the walls undulate. Viewed in superficial sections the lateral walls of epidermis are prominently undulate on both faces of the blade; in cross-section epidermis is thin-walled on both faces, with about the same lumen; stellate, and simple, unbranched hairs are frequent on both faces of the blade, the simple being unicellular, very long, and sharply pointed. There is one layer of palisade-tissue (FIG. 5), which is very open, and the cells are very short and much broader under the epidermis than where they touch the pneumatic tissue; the pneumatic tissue is of three to four layers of oblong to roundish cells with wide intercellular spaces; the chlorenchyma, especially the palisade-tissue, is rich in chlorophyll. The structure of this palisade-tissue is very different from the typical, because the cells are mostly of a funnel-like shape, as shown in the figure (FIG. 5). In describing the system of assimilation Haberlandt¹ calls special attention to this structure, the funnel-shaped cells, but according to this author, it is generally in the pneumatic tissue that this cell-form is represented in order to connect with a larger or smaller fascicle of true palisade cells so as to conduct the assimilated substances to the parenchyma sheaths of the mestome-strands. By Haberlandt these funnel-shaped cells are therefore called "Sammel- oder absorption-zellen," *i. e.* receiving cells; he cites several plants showing this structure of the uppermost stratum of the pneumatic tissue, for instance some ferns, but also several

¹ Haberlandt, G. *Physiologische Pflanzenanatomie*. Leipzig, 1896, p. 246 seq.

Dicotyledons: *Ficus*, *Juglans*, *Pulmonaria*, *Eranthis*, etc. But with regard to the typical palisade cells being replaced by funnel-shaped as in our *Hamamelis* (FIG. 5) Haberlandt attributes this structure to sciaphilous plants especially, where the great width of the cells, directly beneath the ventral epidermis, favors an increased assimilation in the diffuse light of the shady environment. Several instances of this particular structure have been described and partly figured in our paper dealing with: Sciaphilous plant-types,¹ among these: *Orchis rotundifolia* Pursh, *Aster divaricatus* L., *Aristolochia Serpentaria* L., *Lepidagathis alopecuroides* R. Br., *Spiraea Aruncus* L., *Amphicarpaea monoica* (L.) Ell., *Stellaria pubera* Michx., etc. The very open structure of the pneumatic tissue in *Hamamelis* recurs in several sciaphilous plants, and by containing chlorophyll, even to a limited extent, it thus performs two functions: aerating and assimilating.

There is another peculiar structure to be observed in the chlorenchyma, namely the development of long, thick-walled sclereids (FIG. 7), which, however, are more frequent in the leaves of the mature tree. Haberlandt (l. c. p. 141) describes the sclerenchyma and the various types of sclereids (a term proposed by Tschirch) which have been observed; he distinguishes between "brachy-, macro-, osteo- and astro-sclereids" in accordance with their shape. Of these forms the more or less isodiametric sclereids, the brachy-sclereids, are the most common, known especially from the pericycle of the stem of many herbaceous and woody plants, from the fruits of *Pomaceae*, and from the tuberous roots of *Dahlia*, *Paeonia* etc.; by Solereder² they are called "stone-cells." The sclereids in our *Hamamelis* represent the type "macro-sclereids," and are known from the leaves of many plants, more seldom from the stems (cortex and pith). Solereder calls this type "Spicular-zellen" (l. c. p. 919), and he enumerates the families in which they have been observed. The function of the sclereids is, according to Haberlandt, of a local, mechanical nature. This term proposed by Tschirch is more natural than that of some other authors, who under the category "idioblasts" include stone-cells, crystal-cells, oil-cells, resin-cells, etc., for instance Sachs,³ Strassburger,⁴ and others.

¹ Beihefte Bot. Centralbl. Vol. 44. Dresden, 1927.

² Solereder, Hans. Systematische Anatomie der Dicotyledonen. Stuttgart, 1899, p. 966.

³ Sachs, Julius. Lehrbuch der Botanik, 4th ed. Leipzig, 1874, p. 85.

⁴ Strassburger, E. Lehrbuch der Botanik. Jena, 1894, p. 71. (Strassburger, Noll, Schenck and Schimper).

The midrib forms an obtuse keel on the lower face of the leaf-blade, and contains a thin-walled water-storage-tissue of two to five strata, surrounding the single, arch-shaped mestome-strand. No endodermis was observed, but the leptome and the hadrome have a support of several layers of stereome forming two separate arches; the hadrome contains no libriform. A few single crystals were observed in the dorsal part of the water-storage-tissue. The lateral, thin veins are surrounded by green parenchyma-sheaths, inside of which some few stereids may be noticed on the leptome-side. The cells of the parenchyma-sheath border on the palisade- and the pneumatic-tissue.

The leaf of the full grown tree or large shrub shows the same structure of the the cuticle, epidermis and stomata as the primary leaf of the seedling; stellate hairs of two types, *viz.* four-armed with very thin cross-walls, and ten-armed, which are a little shorter and more thick-walled than the four-armed, and lack the cross-walls; of these types the former is the most frequent on the dorsal face, while the ten-armed occur on both faces of the blade. The chlorenchyma is developed as a typical palisade tissue of one layer (*P* in FIG. 7) of high cells rich in chlorophyll, and covering a relatively compact pneumatic tissue of about four to five strata with only a little chlorophyll; large macro-sclereids (FIG. 7) are frequent, extending from the ventral epidermis to the dorsal, and, sometimes, breaking through this; some few single crystals were observed in the palisade-tissue. The midrib (FIG. 8) forms a large, obtuse keel on the dorsal face of the leaf-blade, containing three strata of hypodermal collenchyma around the keel, and on the narrow, upper face, the chlorenchyma does not extend across the midrib, being interrupted by a large water-storage-tissue, surrounding a large stele, circular in cross-section, and an arch-shaped, collateral mestome-strand above this, and close to the ventral epidermis. A closed sheath of stereome in five to six layers surrounds the stele and the single mestome-strand; the leptome of the latter shows the normal, dorsal position; the center of the stele is occupied by a broad pith, containing many single, but only a few aggregated crystals of calcium-oxalate; similar crystals were also observed in the water-storage-tissue, besides macro-sclereids. This singular structure of the midrib recurs in the lateral veins, the secondaries, with the exception that there is a small opening on the ventral face of the stele, and that the ventral, arch-shaped mestome-strand above is wanting. In following the structure of the midrib towards the apex

of the leaf-blade, the composition is very different, there being only an arch of mestome, surrounded by a large, thin-walled parenchyma, and a completely closed sheath of stereome; a narrow arch of pith is located between the hadrome and the ventral portion of the stereome.

The petiole of the mature leaf is almost cylindric, and very hairy near the base of the blade. The cuticle is smooth, and the epidermis is of small, thick-walled cells. Three to five hypodermal strata of collenchyma surround a thin-walled cortex of about eight layers, very compact, and containing chlorophyll and crystals, single as well as aggregated, the former being most abundant near the stereomatic pericycle, which surrounds a central stele, corresponding exactly with that of the midrib of the leaf-blade.

When comparing the structure of the cotyledons, the primary leaf of the seedling, and the leaf of the mature tree, we observe the following points of interest. The petiole of the cotyledon contains three collateral mestome-strands, located in one band, while a typical stele occurs in the petiole of the primary leaf and of the leaf of the tree. The chlorenchyma consists of one layer of short palisade cells with several funnel-shaped, and of eight strata of open, pneumatic tissue in the cotyledon; of one layer of short, funnel-shaped cells covering a pneumatic tissue of three to four layers with wide intercellular spaces in the primary leaf; and of one layer of typical, compact palisades covering a pneumatic tissue of four to five compact strata in the leaf of the tree. Macro-sclereids were observed in the chlorenchyma of the primary leaf and of the leaf of the tree, but not in the cotyledons. The midrib of the cotyledon consists of one arch-shaped, collateral mestome-strand with a dorsal water-storage-tissue; that of the primary leaf shows the same structure, while in the leaf of the tree the midrib represents a stele, circular in cross-section, with a ventral, collateral mestome-strand, and with a large, dorsal water-storage-tissue. The crystals of calcium-oxalate are distributed as follows. Aggregated as well as single, rhombic were found in the cortex of the petiole of the leaf of the tree; only single crystals were observed in the chlorenchyma of the leaf of the tree, and in the water-storage-tissue of the midrib in the primary leaf; many single and a few aggregated crystals were observed in the pith of the stele in the leaf of the tree, and in the dorsal water-storage-tissue of same. No crystals were found in the cotyledons, nor in the petiole of the primary leaf.

We have thus in the seedling of *Hamamelis Virginiana* an illustra-

tion of the early appearance of some of the more important structures, noticeable in the root, stem and foliage. We have seen the development of cork and a secondary cortex in the root at the close of the first season, while stereids and brachy-sclereids do not appear in the secondary cortex before the roots are several years old. The development of stellate hairs begins on the epicotyl, while the cork, and the differentiation of the cortex into collenchyma and ordinary parenchyma already begins in the hypocotyl. The pericycle being purely stereomatic in the seedling, but interspersed with brachy-sclereids in the branches of the tree. The appearance of aggregated crystals in the epicotyl, and of single in the apical internodes of the seedling. With regard to the foliage we have seen that the cotyledons and the primary leaf lack a typical palisade-tissue, while such is well represented by the leaves of the tree; moreover the appearance of macro-sclereids in the chlorenchyma of the primary leaf, recurring more frequently in the foliage of the tree; the singular structure of the midrib of the leaf of the tree representing a stele, while that of the cotyledons and the primary leaf contains only a single, arch-shaped mestome-strand; finally the occurrence of single crystals in the water-storage-tissue of the primary leaf, but of both single and aggregated in the various tissues of the leaves of the tree.

If we compare the structure of *Hamamelis* with that of *Liquidambar*, the total absence of secretory ducts from the former, and their presence in the latter constitutes an anatomical character of importance, and more so than the development of sclereids in the leaves of *Hamamelis*. It was principally upon the basis of the system of secretory ducts in *Liquidambar* and *Altingia* that Van Tieghem¹ segregated these genera from *Hamamelideae* (*Hamamelis*, *Rhodoleia*) as a small, very distinct group of very doubtful affinity; for even if the structure of the stem and leaf resembles that of *Dipterocarpeae* and *Simarubaceae*, the root-structure does not agree with these. When combining these anatomical characteristics with the floral structure as represented by *Liquidambar* on the one side, and by *Hamamelis* on the other the segregation appears a very natural one. But considered by itself alone the anatomical structure, in this case the presence of ducts, would hardly be sufficient for warranting such segregation, because the development of secretory cells as well as secretory ducts may characterize all the members of certain families, or only

¹ Van Tieghem, Ph. Second mémoire sur les canaux sécréteurs des plantes. Aun. d. sc. nat. Bot. Série 7, Vol. 1. Paris, 1885, p. 86.

some of the genera or species. For instance, in the *Compositae* endodermal ducts occur in many of the *Tubuliflorae*, in several of the *Labiatiflorae*, but only in a few *Cichoriaceae*; in the *Cornaceae* ducts are only known from *Mastixia*, in the *Caesalpiniceae* from *Eperna* and *Copaifera*, etc.

CLINTON, MARYLAND

EXPLANATION OF PLATES 206 AND 207.

(All the figures are of *Hamamelis Virginiana* L.)

PLATE 206. FIG. 1, leaf of the tree; two-thirds of the natural size. FIG. 2, the seedling; natural size. FIG. 3, second proper leaf of a seedling; natural size. FIG. 4, cross-section of the hypocotyl of a seedling; Ep = epidermis, Co = cork, Coll. = collenchyma; $\times 480$. FIG. 5, cross-section of the primary leaf of a seedling; Ep. = ventral, Ep* = dorsal epidermis, P = ventral chlorenchyma, P* = pneumatic tissue; $\times 480$.

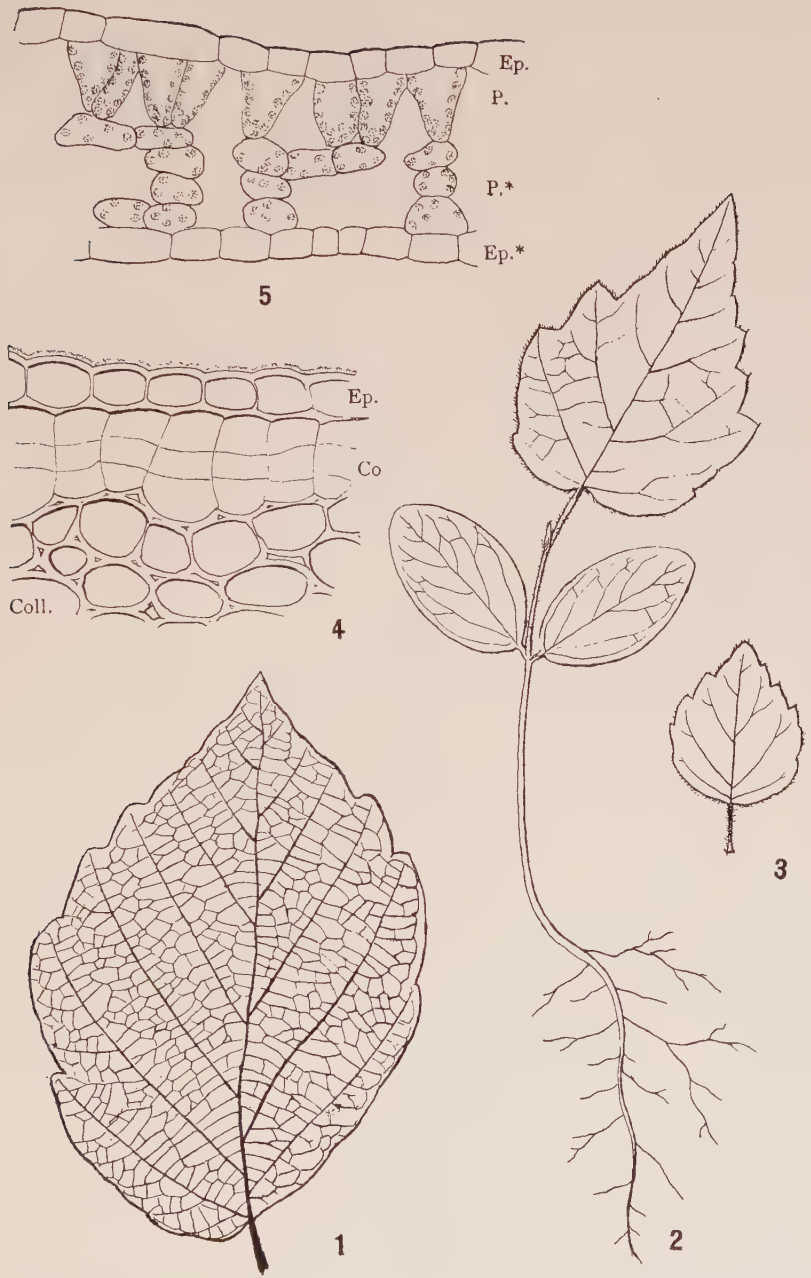
PLATE 207. FIG. 6, cross-section of a branch in its first year, letters as in fig. 4; $\times 480$. FIG. 7, cross-section of a leaf of the tree, showing a macrosclereid; letters as in FIG. 5; $\times 480$. FIG. 8, cross-section of the midrib of a leaf of the tree, Ep = ventral, Ep* = dorsal epidermis. The large, obtuse keel contains a stele of mestome surrounded by a sheath of stereome, bordering on the leptome, and outside this is a large-celled water-storage-tissue, surrounded by strata of peripheral collenchyma. Above the stele, close to the ventral epidermis, is a small, collateral mestome-strand; $\times 60$.

PECULIAR ASPECTS OF THE NEW ENGLAND DISTRIBUTION OF ARCEUTHOBIMUM PUSILLUM

R. J. EATON

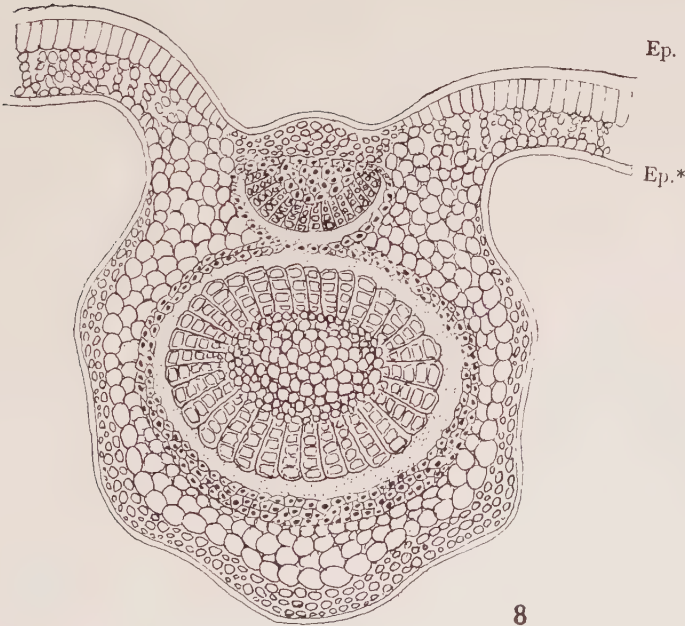
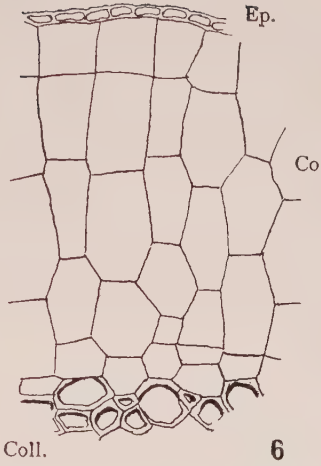
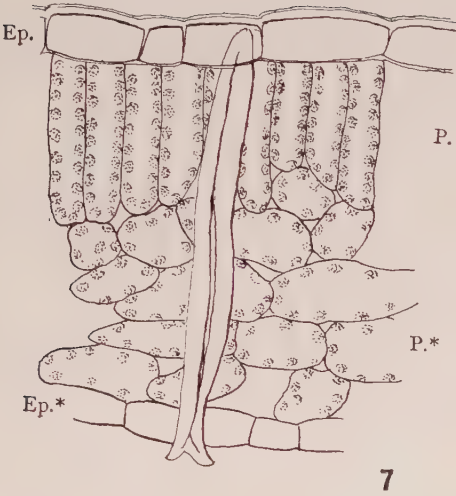
THERE is a diminutive roadside bog in Concord, Massachusetts, where Thoreau first discovered *Ledum groenlandicum* Oeder seventy-five years ago. Typical associates are also present, such as *Picea mariana* (Mill.) BSP., *Andromeda glaucophylla* Link, *Kalmia polifolia* Wang. and the like.

During a brief stop at this place last summer, Ludlow Griscom called my attention to the diseased appearance of one of the half dozen young specimens of *Picea mariana* which have survived sundry wood cutting and draining operations. On close examination, the disease proved to be a heavy infection of *Arceuthobium pusillum* Peck. Strangely enough we could find no infection on any other spruce despite the fact that the branches of the nearest neighbor were actually interlocked with those of the diseased tree. Thus does the survival of the dwarf mistletoe in this bog, to say nothing of the entire Concord region, hang by a very slender thread!



Theo. Holm del

HAMAMELIS VIRGINIANA.



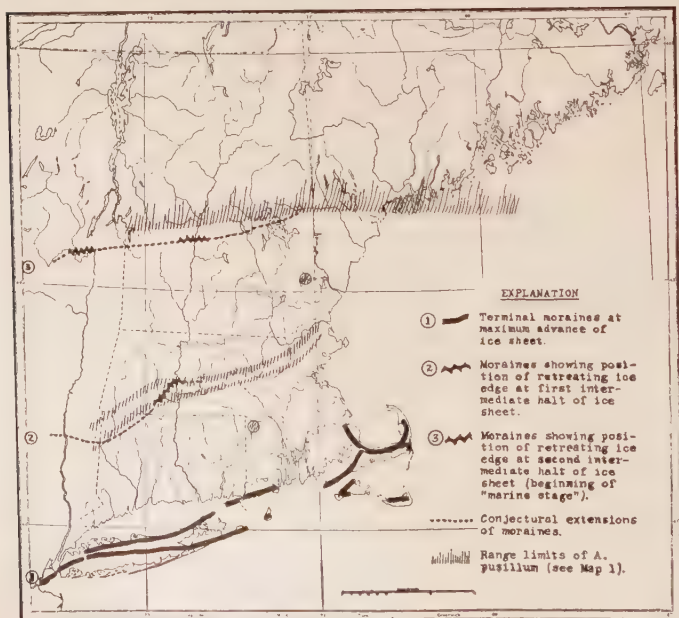
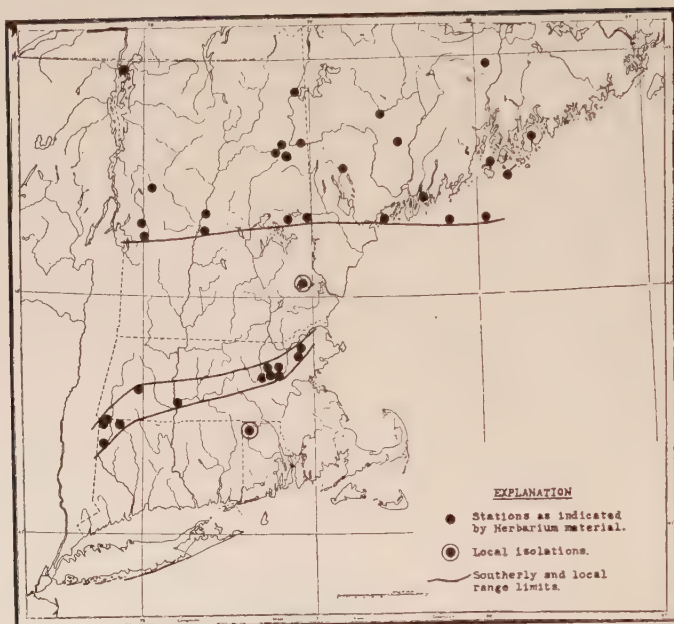
Theo. Holm del.

HAMAMELIS VIRGINIANA.

Returning to the bog on September 29, 1930, for fresh material and for further examination of other spruce trees in the vicinity, I collected excellent fruiting specimens, as well as staminate plants, the identity of which has been confirmed by Dr. J. H. Faull. The occurrence of both sexes of this dioecious parasite on a single host tree is exceptional (Thoday & Johnston, Ann. Bot. p. 393, XLIV, April, 1930). Close scrutiny failed to reveal the slightest trace of infection on any other spruce, which is the more surprising in the light of the presence of fertile plants.

An interesting symposium on dwarf mistletoe was published in RHODORA for January, 1900, with excellent plates illustrating the external characteristics of the plant, its effect on the host and the method of seed dissemination. It is astonishing to learn that the parasite was unknown to science prior to 1871. It was considered an extremely rare and local plant as recently as 1899. At present it is regarded as widely distributed throughout the limit of its range, occurring in the six New England states, New York, New Jersey (*L. Griseb.*), Pennsylvania, Michigan, Wisconsin, and northward. On the recent authority of Thoday & Johnston (*supra*), J. H. Faull and others, *A. pusillum* occurs chiefly as an endophytic parasite in the tissues of its principal host, *Picea mariana*, but can spread to *P. canadensis* (Mill.) BSP., *P. rubra* (Du Roi) Dietr., and very exceptionally to *Larix laricina* (Du Roi) Koch. Externally, it appears to be confined to a very definite region of the infected twigs. Full-grown aerial shoots in August with ripening fruits occur mainly on the three-year old stem and occasionally on the upper part of the four-year old stem. Shoots with nearly mature flowers occur on the two-year old twigs. The parasite is not visible as a rule on one-year old or current year growth, although its endophytic system grows forward keeping pace each season with the growth of the host twig. The ovary of the mature plant contains a single ovule covered with a sticky glutinous substance which facilitates transportation by birds and lodgement on a host twig. Faull asserts that germination occurs only on live twigs of the host, and apparently only at particularly favorable spots on the twig. Such a condition indicates that unusual germination factors are necessary for the propagation of the species. This conclusion is of importance in judging the significance of certain observations in subsequent paragraphs of this article.

In view of the fact that *Arceuthobium* is very easily overlooked the



Map 1 (upper). Distribution of *Arceuthobium pusillum* in central and southern New England.

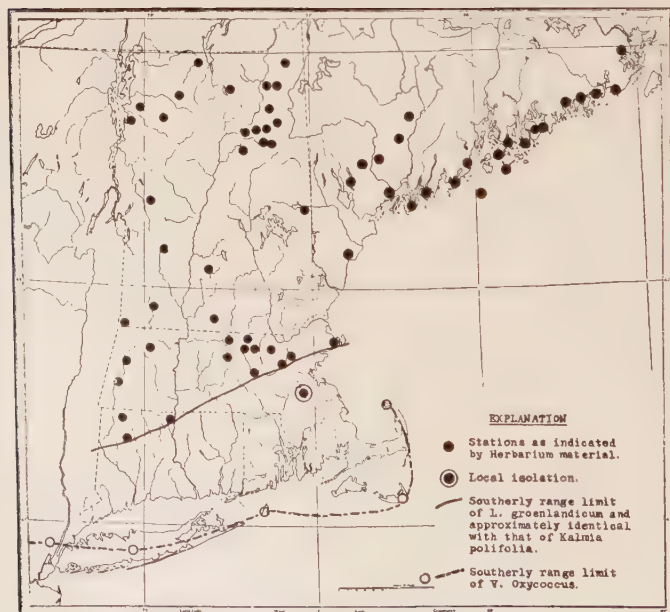
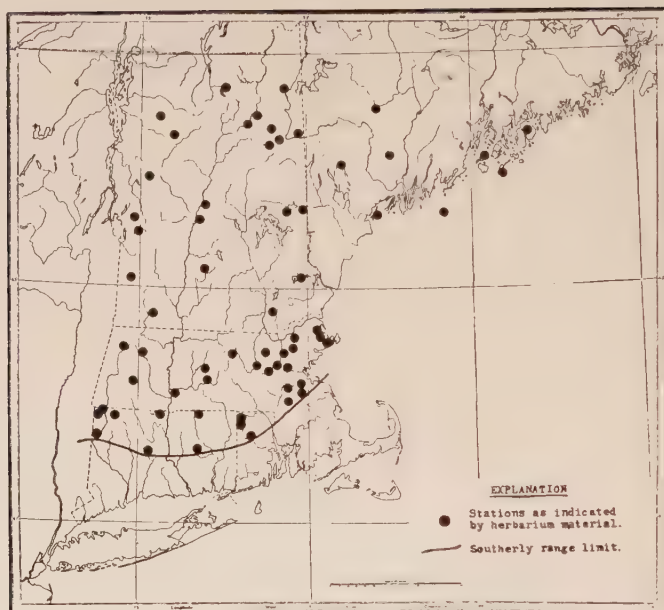
Map 2 (lower). Position of Moraines of the last (Wisconsin) advance of the Pleistocene glaciations (after Antevs) compared with southern limits of *A. pusillum*.

existing records of its occurrence in southern New England, as determined by the specimens filed at the Gray Herbarium, at Arnold Arboretum, and in the herbarium of the New England Botanical Club,¹ perhaps are not particularly significant. The remainder of this article must be read with this clearly in mind. Exclusive of Maine, where the plant is widely distributed, there are collections of dwarf mistletoe from only twenty-eight New England towns (MAP 1). Of these, nine are from Massachusetts, four from Connecticut, and one from Gloucester, Rhode Island. Curiously enough, if we consider the Gloucester station as a local isolation, the remaining thirteen southern New England stations form a narrow straight belt, closely paralleling and seventy-five miles north of the terminal moraine² of the last glaciation. This belt extends from Andover, Massachusetts, to Salisbury, Connecticut, through Wilmington (Massachusetts), Concord, Acton, Lancaster, Clinton, Boylston, Springfield, Becket, Norfolk (Connecticut) and Kent. The new Concord station is the most southeasterly one in Massachusetts. To the northward, there is a wide gap of 80-100 miles from which we have no herbarium material except from a single station at Nottingham, New Hampshire. The most southerly limit of this secondary belt (from present available information) is marked by the line: Matinicus Is. (Maine), Monhegan Is., Great Chebeague Is., Effingham (New Hampshire), Lebanon, Rutland (Vermont).

At the present writing there appears to be no reasonable explanation for this curious representation in the three herbaria consulted other

¹ A thorough analysis of the complete ranges of the plants discussed in this article may not be attempted without reference to all the important herbaria in North America. Lack of time and opportunity prohibits for the present an analysis of the entire North American range of *A. pusillum*, such as I have made for New England. In fact, it is probable that local collections in other sectors of the range are not sufficiently extensive to warrant an attempt at piecing together the whole picture. A continuous series of specimens by townships is the ideal data from which to work up a study of this sort. In all probability the nearest approach to this ideal, as far as any large local area is concerned, may be gained by reference to the New England material contained in the three botanical establishments which I have consulted. The precise distribution of plants within the limits of central and southern New England is sufficiently well known to justify a certain degree of reliance on any conclusions derived from existing records within this area.

² Following Antevs (The Last Glaciation, p. 164; Am. Geog. Soc. 1928) I have sketched the three southerly positions of the retreating Wisconsin ice which represent halts of sufficient duration to have produced terminal moraines (MAP 2). It is indeed remarkable that the primary and secondary range-limits of *Arceuthobium* are substantially on the identical lines indicated by Antevs as major intermediate resting stages during the retreat of the ice sheet. No explanation is offered, if indeed any rational explanation is possible.



Map 3 (upper). Distribution of *Picea mariana* in central and southern New England.

Map 4 (lower). Distribution of *Ledum groenlandicum* in central and southern New England (Maine stations incomplete) and the southerly range-limit of *Vaccinium oxycoccus*.

than the merest coincidence. Hence, records accompanied by vouchers from other localities in southern New England would be welcome in order that the true distribution may be determined. However, should it become an established fact that *Arceuthobium* occurs in New England south of $43^{\circ} 50'$ parallel only in an isolated narrow belt (except for the two anomalous outposts previously mentioned at Gloucester, Rhode Island, and Effingham, New Hampshire), a problem at once arises which may have subtle ramifications.

Primarily, the distribution of *Arceuthobium pusillum* is determined by that of its two principal hosts, *Picea mariana* and *P. canadensis*. From the meagre evidence in hand, there seem to be striking inconsistencies in the ranges of hosts and parasite. For instance, it is not apparent why *Arceuthobium* should not occur, if indeed such is the case, in the general region, Ashburnham, Ashby, Rindge and Winchendon where *P. mariana* is abundant in the numerous sphagnum bogs of that ill-drained divide between two water-sheds. Again, it is strange that the scattering of spruces in three other sphagnum bogs in Concord should not harbour the parasite, all the obvious ecological conditions being just as satisfactory as at the *Ledum* station.

Some secondary set of influences must operate to restrict the occurrence of *Arceuthobium* to a range strikingly localized in comparison with that of *Picea*. Specimens of black spruce (MAP 3), for example, are noted from twenty-two towns in six counties in Massachusetts, from Ipswich and Foxboro in the east to Adams and Becket in the Berkshires. There are three stations represented from Rhode Island and eight from Connecticut. Its southerly limit of distribution runs through Canton (Massachusetts), Foxboro, Scituate (Rhode Island), Southington (Connecticut) and Kent, for the most part exactly paralleling the limit of range of *Arceuthobium* but about thirty miles to the southward. Obviously, some limiting factors are at work to prevent the dwarf mistletoe from occupying a range essentially coincident with that of black spruce.

There are two curious facts or coincidences concerning *Arceuthobium* which may be suggestive. The first has already been alluded to: at Concord the parasite shows no disposition to spread from the infected spruce to its contiguous neighbor even though the branches of both trees are more or less interwoven. Such a condition at once suggests the remote possibility of a symbiotic association of some sort, although I must confess that the idea is novel to say the least when

applied to vascular parasites. Improbable though it may be, it is not inconceivable that *Arceuthobium* is associated with and perhaps dependent for its complete development on some fungus or bacteria which requires two hosts for the completion of its life cycle. Perhaps the parasite will attack only those individual specimens of spruce and larch which previously for some reason have become weakened. Following out this latter line of thought, it may be found that a small percentage of the host trees are subject to some fungus or other primary disease which permits *Arceuthobium* to gain a foothold. As the southern limit of *Picea* is approached, individual specimens become more and more sparsely distributed in locally isolated bogs. It would follow, logically enough, that the numbers of weakened host trees would diminish and perhaps disappear entirely at the extreme southerly range-limit where stations for spruce are relatively widely separated. By postulating a primary disease to which *P. mariana* is the most and *L. laricina* the least susceptible of the four known hosts of *A. pusillum*, we provide a simple explanation for the extraordinary discrimination which the parasite displays. In this connection, it is pointed out that I found only one specimen of *A. pusillum* on *L. laricina* (Arnold Arboretum: Kent, Connecticut, Austin & Fames, 11 May, 1903) among all the material which I examined in the three herbaria despite the fact that the larch is probably just as common as *P. mariana*, if not more so, in Massachusetts, Rhode Island and Connecticut.

The second fact relates to an evident similarity in the ranges of *A. pusillum* and certain northern heaths, notably *Kalmia polifolia* and *Ledum groenlandicum*. A detailed range-study of the entire series of the normal sphagnum bog associations, including the cryptogams, should be made before we are justified in attaching much significance to this phenomenon. The occurrence of *Ledum* and *Arceuthobium* in close association in a small bog in Concord along the extreme southeastern limit of range of each species, and nowhere else so far as I know within a radius of approximately eight miles, seemed so curious that I plotted the southern New England distribution of *Ledum* (MAP 4). Except for two locally isolated stations, at Canton, Massachusetts, and Litchfield, Connecticut, and for the *Arceuthobium* station at Glocester, Rhode Island, the southeasterly limits for both species coincide in a most striking fashion. Subsequently, I tested the distribution of four other conspicuous bog plants, in order

to avoid placing undue emphasis solely on *Ledum* as possessing a definite relationship to the occurrence of *Arceuthobium* and *Picea*. The species selected were: *Eriophorum spissum* Fernald, *Kalmia polifolia* Wang., *Andromeda glaucophylla* Link, and *Vaccinium Oxyccoccus* L. Of these four random species, the range of *K. polifolia* alone exhibits features comparable to that of *Ledum*, although it occurs much more commonly along its southern limit than either *Arceuthobium* or *Ledum*. Unlike the latter, it is locally isolated at Glocester (Rhode Island) in close association with *Arceuthobium*.

Of the remaining three species, *Eriophorum spissum* occurs at Provincetown (Massachusetts), Glocester (Rhode Island), and Waterbury (Connecticut) as the southern limit of its range, thus bearing no similarity to that of dwarf mistletoe. *Andromeda* exhibits a range comparable to that of *Picea mariana*, from Norfolk County in eastern Massachusetts through Glocester (Rhode Island) to Danbury in southwestern Connecticut. *Vaccinium Oxyccoccus* is likely to occur wherever suitable sphagnum bogs exist and is known from Provincetown, Nantucket, Block Island and Ronkonkoma (Long Island, New York) along a line substantially coinciding with the Wisconsin terminal moraine.

The suggestion that *Arceuthobium* may depend in some obscure manner on the presence of *Ledum*, *Kalmia*, or for that matter any other bog associate, cannot be considered very seriously without much more evidence. Copious as it is, the material examined is too meagre to warrant generalization.¹ A more accurate knowledge of the true ranges, past and present, of the various plants under discussion is

¹ Much emphasis has been laid on mere coincidence resulting from insufficient field data as a probable interpretation of my observations. As a matter of fact, I feel that coincidence is effectually ruled out by the law of chances. Assuming that the distribution of *Picea* is the sole factor in determining that of *Arceuthobium*, except as modified by the less aggressive nature of the latter, owing to limitations of seed dissemination, fecundity, and kindred restrictive influences, one would certainly expect to find scattering stations of *Arceuthobium* throughout the entire range of *Picea mariana* and *P. canadensis*. Because of the insignificant aspect of *Arceuthobium*, we properly might expect a far greater representation of spruce than of dwarf mistletoe in our herbaria, but we also properly would expect to find no essential discrepancies in distribution. The three herbaria contain specimens of *Arceuthobium* from about fifty New England stations and perhaps three times that number of *Picea mariana*. If mere chance is the sole distributional factor the mathematical chances are indeed slim for the fifty *Arceuthobium* stations to fall into two well defined belts which appear to be correlated with several other sets of phenomena: (1) parallelism, (2) range limits of certain bog associations, (3) glacial moraines. Any rational explanation, other than coincidence, is difficult to imagine, considering our present incomplete understanding of the problem. Nevertheless our instinct must prompt us to reject coincidence as altogether too unlikely.

necessary before mere suspicions may become dignified by serious study. My observations are most useful, possibly, as tentative leads for the cryptogamic specialist.

However far-fetched these suspicions may be, it remains true that there are one or more unknown limiting factors in the southerly occurrence of *A. pusillum* which are unrelated to the distribution of its principal host. This fact does not appear to have been pointed out heretofore, and is at present unexplained so far as I am aware. Perhaps microscopic studies of host and parasite will shed some light on the question. I have already alluded to the possible existence of some fungus, requiring two hosts for the completion of its life cycle, which enables the mistletoe to gain a foothold on a previously weakened host tree. It is conceivable also that the parasite may vegetate in a purely endophytic state under certain conditions, awaiting some necessary stimulus for the development of aerial (and visible) shoots capable of reproducing the species. Other wild guesses stimulate the imagination. For instance, on the likely assumption that seed dissemination is accomplished to a certain extent through the agency of birds to whose feet the sticky seed readily adhere, it might be profitable to investigate the casual and permanent fauna and flora of birds' feet, particularly of those species, such as the northern finches, which occasionally winter as far south as southern New England.¹

It may be significant that another species of the genus *Arceuthobium* presents ecological peculiarities of a baffling nature. An interesting study of the northwestern *A. americanum* Nutt. on *Pinus Banksiana*² has been just brought to my attention, fortunately in time to permit a brief allusion to certain points which are pertinent to the present discussion. In this study it is shown that *A. americanum* tends to infect only trees in certain types of habitat, that it is very slow to develop new infections on healthy trees, showing evident preference for trees fifteen years or more old, and that the production of mature fruits in moist situations is very effectually checked by the parasitic

¹ This suggestion is not very helpful in attempting to explain the presence of *Arceuthobium* in the narrow isolated band extending southwesterly across Massachusetts and northwestern Connecticut. Similarly, the fairly regular occurrence of *Ledum* and *Kalmia polifolia* throughout the "gap" in northern Massachusetts, southern Vermont and southern New Hampshire would appear effectually to dispose of any idea that these plants are interdependent. Taking everything into consideration, it does not seem safe to place too much reliance on the supposed gap in the New England distribution of dwarf mistletoe—at least until a more extensive field survey has been made in the barren area.

² Dowding, E. S. Ecology of *Arceuthobium americanum* Nutt. *Journal of Ecology*, XVII. 96-105 (Feb. 1929).

fungus *Wallrothiella arceuthobii* Ros., "a disease which flourishes best in damp shaded places."³ The present importance of this rests in the fact that *A. pusillum* is a closely related species of the same genus and may be expected to exhibit analogous peculiarities and susceptibilities. Hence, it is all the more probable that the curious distribution of *A. pusillum* in New England points to a problem worthy of the attention of a specialist.

BOSTON, MASSACHUSETTS.

DWARF MISTLETOE AND OTHER PLANTS NEW TO NEW JERSEY.—

From 1919 to 1923 the writer had the great good fortune to accompany Mr. Kenneth K. Mackenzie in a long series of summer weekend collecting trips to various parts of New Jersey, and Mr. Mackenzie frequently urged me to record the more unusual and novel finds. We paid particular attention to the higher hills in the northwestern corner of the state in a search for Canadian Zone plants. On June 19, 1920 we explored Pine Swamp, just west of Lake Mashipacong, on the summit of the Kittatinny Ridge in Sussex County, at an altitude of 1200 ft. It proved to be an ideal locality, as there was a quaking sphagnum bog surrounded by black spruce in the heart of the southern end of the swamp. Here were such rarities (for New Jersey) as *Kalmia polifolia* Wang. and *Carex rostrata* Stokes. In the open sphagnum were clumps of *Eriophorum spissum* Fernald (*callitrix* of Gray's Manual), new to the State. The most spectacular event, however, was the discovery of *Arceuthobium pusillum* Peck in some abundance on a considerable number of spruce trees a few minutes after our telling each other that the plant should occur here, if indeed it was ever to be found in the State. The range of the species is here extended south from northwestern Connecticut.

On July 10 the locality was revisited, and we discovered another sphagnum bog in the heart of the north end of the swamp. This bog was a younger one, and contained a small pond in the middle, the border of which was almost unreachable. However, by lying down full length, I was just able to grasp some small clumps of green, equitant leaves, seen from some distance off, which proved to be *Xyris montana* Ries, new to New Jersey. This bog also contained some more *Eriophorum spissum* and a little more Dwarf Mistletoe. Pine Swamp outranks even Budd's Lake as the best of the very few sphagnum bogs in the State.—Ludlow Griscom, Cambridge, Mass.

³ Ibid. 98

A NEW BLACKBERRY FROM NEW HAMPSHIRE

M. L. FERNALD

DURING the summers of 1915 and 1917 I devoted much of my attention to the genus *Rubus* as it occurs in central and northern New Hampshire, collecting and preparing more than 6000 sheets of material, included under 295 numbers. A full series of the more significant species was sent, at his request, to the late Dr. Ezra Brainerd for study. One species in particular, one of the most characteristic trailing or low-arching and entangling brambles of the Pemigewasset Valley in Grafton County, is the subject of this note. In the 1915 collection it was called by Brainerd *R. Groutianus* Blanchard and material under that name was widely distributed; but, convinced by a study of the 1917 collections that it constitutes a distinct species, Brainerd consistently labeled the later collections "*Rubus severus* Brainerd, ined," and under this name I distributed the duplicates.

In Brainerd & Peitersen's *Blackberries of New England—their Classification*,¹ however, published two years later, no recognition was accorded the species, even as a "hybrid," for Brainerd's notes on the sheets in the Gray Herbarium indicate that it might be sought, if not under the new name *R. severus*, at least under *R. elegantulus* or a cross of that and *R. vermontanus*, var. *viridifolius*; Brainerd's labeling in the Gray Herbarium reading: "Revision by Ezra Brainerd. Jan. 1918. *Rubus severus* Brainerd, ined. Combines the characters of *R. elegantulus* Blanch. with those of *R. vermontanus* var. *viridifolius* Blanch." That Brainerd did not comment on this and much other New England material which he had studied in the herbarium may well have been due to a desire first to see the new species growing. Declining strength and advanced years made such an ambition impossible of fulfillment and *R. severus* has lain unpublished until the present time. In view of Brainerd's conviction, expressed in letters as well as on the labels and wholly coinciding with the field-judgment of the collector, that *R. severus* is a distinct species, it seems desirable to give it this belated publication.

RUBUS severus Brainerd, n. sp. in Gray Herb., arcuans deinde prostratus; turionibus deinde ramosissimis apice radicantibus 0.5–3 m. longis aculeis 2–4 mm. longis rigidis rectis vel curvatis divergentibus vel subretrorsis subulatis basi dilatatis valde armatis, setis glanduliferis sparse intermixtis; foliis quinquefoliolatis longe petiolatis, petiolis

¹ Brainerd & Peitersen, Vt. Agr. Expt. Sta. Bull. 217 (1920).

armatis, foliolis anguste obovatis subcoriaceis acuminatis basi rotundatis glabris vel glabratiss petiolulatis supra nigro-viridibus subtus pallidiviridibus grosse duplicato-serratis 4–13 cm. longis 2–8 cm. latis, petiolulis armatis mediis valde elongatis 1.5–4 cm. longis; foliis trifoliolatis subtus minute pilosis glabratissque foliolis elliptico-obovatis 2–7 cm. longis 1–3.5 cm. latis; inflorescentia racemoso-paniculata vel subcorymbiformi foliosa interrupta 0.5–2.3 dm. longa; rhachibus remote retrorse aculeatis minute pilosis; pedicellis filiformibus 2–5 cm. longis aculeis aciculiformibus remotis setis glanduliferis plus minusve intermixtis armatis; sepalis deltoideo-ovatis caudato-acuminatis 4–8 mm. longis; petalis oblongis 9–11 mm. longis 4–5 mm. latis; fructibus globosis; putaminibus semiorbicularibus 2.8–3 mm. longis 1.6–2 mm. latis valde reticulatis.—Pemigewasset Valley, Grafton Co., NEW HAMPSHIRE: dry thickets and borders of woods, Lincoln, July 28, 1917, *Fernald*, no. 15,754; dry thickets and clearings, North Woodstock, Woodstock, August 7, 1915, *Fernald*, no. 11,765; springy thickets and banks, North Woodstock, August 7, 1915, *Fernald*, no. 11,768 (TYPE in Gray Herb.). dry thickets and roadsides, North Woodstock, July 6, 1915, *Fernald*, no. 11,780; river-gravels, North Woodstock, July 6, 1915, *Fernald*, no. 11,782 (all material of 1915 distributed as *R. Groutianus* Blanchard); dry woods and recent clearings, North Woodstock, August 20, 1917, *Fernald*, no. 15,616; border of sphagnum bog, North Woodstock, August 20, 1917, *Fernald*, no. 15,618; swampy thickets near Lost River, Woodstock, July 31, 1917, *Fernald*, no. 15,752; bushy intervalle, Woodstock, August 3, 1917, *Fernald*, no. 15,806; dry thickets, borders of woods and roadsides, Thornton Gore, Thornton, August 27, 1917, *Fernald*, nos. 15,608, 15,745; dry thickets, clearings and roadsides, Thornton Gore, Thornton, July 28, 1917, *Fernald*, no. 15,753.

From *Rubus elegantulus* Blanchard, near which Brainerd seems to have placed *R. severus*, it is at once distinguished by its much more prostrate canes, having much more abundant prickles with occasional gland-tipped setae interspersed; subcoriaceous foliage, with less sharp serration; more prickly and usually glandular-setulose pedicels; smaller flowers; and drupelets with narrower stones. *R. elegantulus*, as shown by Blanchard's abundant material, is upright, without glands on young canes or inflorescences; the prickles rather remote; the serration of the membranaceous 5-foliolate leaves very slender and elongate (much as in *R. recurvans* Blanchard); the pedicels more pilose, either unarmed or bristly but not glandular; the petals about 1.5 cm. long, 5–7 mm. broad; the stones of the drupelets broadly ovoid or suborbicular.

Only in its trailing or low-arching habit and its often branching corymbiform inflorescence is *Rubus severus* closely approached by

R. vermontanus, var. *viridifolius*. The latter has acicular, not broad-based and hard, crowded prickles on the much more slender canes; its leaves are thinner and, even in the largest 5-foliolate leaves, the longest petiolule is only 0.7–2.5 cm. long; the longest fruiting pedicels only 2–3 cm. long, more abundantly acerose and glandular-setose.

Rubus Groutianus Blanchard, as shown by the Blanchard material in the Gray Herbarium, differs at once from *R. severus* in its more slender canes with more crowded and strongly recurving arched and more acicular prickles, without intermixed glands; much smaller leaves, the middle petiolule of the 5-foliolate leaves only 0.5–1.5 cm. long; the inflorescence copiously setose, with pedicels at most 1.5–2.5 cm. long; the stones of the drupelets suborbicular or broadly ovate.

GRAY HERBARIUM.

Volume 33, no. 387, including pages 65 to 80 and plate 205, was issued 7 March, 1931.

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